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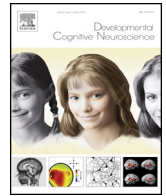
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Review

Social re-orientation and brain development: An expanded and updated view

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ABSTRACT

Social development has been the focus of a great deal of neuroscience based research over the past decade. In this review, we focus on providing a framework for understanding how changes in facets of social development may correspond with changes in brain function. We argue that (1) distinct phases of social behavior emerge based on whether the organizing social force is the mother, peer play, peer integration, or romantic intimacy; (2) each phase is marked by a high degree of affect-driven motivation that elicits a distinct response in subcortical structures; (3) activity generated by these structures interacts with circuits in prefrontal cortex that guide executive functions, and occipital and temporal lobe circuits, which generate specific sensory and perceptual social representations. We propose that the direction, magnitude and duration of interaction among these affective, executive, and perceptual systems may relate to distinct sensitive periods across development that contribute to establishing long-term patterns of brain function and behavior.

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1. Introduction

Humans evolved in an environment where integration with the social world was critical for survival. Because many factors moderate social dynamics (e.g., dominance relations, alliance formation, cooperation, deception (de Wall, 1996)), the need to maintain social cohesion under such complex conditions necessitated the dedication of substantial neuronal resources to processing social signals in the environment (Pinker, 2002; Shultz and Dunbar, 2007; Dunbar,

2012). Social cognition, like many complex cognitive processes, is not fully functional at birth, but rather matures slowly across development. One remarkable feature of human social behavior, and one that we believe is a key aspect of normative maturation, is the dramatic change in social focus across development.

Social behavior is the culmination of input from many neural networks that mediate different aspects of responding to various classes of social stimuli or contexts (Kennedy and Adolphs, 2012). For example, distinct brain networks have been identified for social processes such as motor mimicry (Gallese et al., 2004), joint attention (Happe and Frith, 2014), mentalizing (Saxe and Baron-Cohen, 2006), empathy (Singer and Lamm, 2009), fairness (Güroglu et al., 2011), social bonding (Insel, 2010), and even deception (Yang et al., 2014). Thus, the neural mechanisms underlying social behavior do

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not reflect a single “social brain”, but rather distinct neural circuits that are implicated in fundamentally different and dissociable functional brain processes that evolve and adapt to the social demands of a given environment and a specific phase of development. In a previous review on adolescent neurodevelopment, we argued that the brain processes governing social behavior could be parsed into three broad functional clusters or nodes: the perceptual node; the affective node; and the cognitive-regulatory node (Nelson et al., 2005). This provided a framework for mapping changes in social behavior during adolescence onto maturational changes that take place in the brain. The present paper has two primary goals. The first is to expand the scope of this social re-orientation perspective beyond adolescence to encompass a number of other inflection points in social development. The second is to update the empirical evidence described in the original review and highlight important gaps that need to be addressed in future work.

2. Beyond adolescence: other periods of social re-orientation

We believe at least five distinct social phases occur in development, each of which can be largely defined by the social target and type of social behavior expressed. During *infancy*, sociality primarily consists of engagement with the mother/caregiver. In the *juvenile phase* between weaning and puberty, the mother–infant dyad is gradually replaced with peer-focused play behavior, while maintaining the mother/caregiver as a base. In the *adolescent phase* between puberty and full maturity, social behavior transitions to full integration with larger groups of peers. This transitions into the *reproductive/intimacy* phase, which is accompanied by social bonding and reproductive behavior. Finally, in the *mature adult phase*, social behavior is characterized by interactions within a relatively stable multigenerational group, with the expression of intimate relations, and directed care of offspring. Although this developmental pattern is not universal, it is widely expressed among most primates and in many socially living mammalian species (Hinde and Spencer-Booth, 1967; Biben, 1983; Panksepp et al., 1984; Pusey and Packer, 1987; Spinka et al., 2001; Ekernas and Cords, 2007; Konner, 2010; Zhang et al., 2012). We believe the conservation of this pattern of social phases across development likely indicates that the brain plays an important role in shaping maximally adaptive social behavior.

An important feature of social behavior in each of these phases is that within phase social engagement is highly motivated. Individuals will energetically seek out the developmentally appropriate form of social behavior and they will experience distress when this target is impeded. Highly motivated social engagement is directed at caregivers in infancy, at playmates during the juvenile phase, at integration with peers during adolescence, at potential mates during early adulthood in the social intimacy phase, and at offspring and stable group members in the mature adult phase (Hennessy et al., 1995; Rubin et al., 2010; Trezza et al., 2011; Abrams et al., 2013; Hostinar et al., 2015). This motivation facilitates attention to and behavioral engagement with specific social contexts at developmentally appropriate times. There is even some indication that, like other motivated behaviors, phase specific social behaviors might be under homeostatic control with built-in patterns of compensatory drives and satiation. For instance, periods of maternal separation interspersed with brief, rather than extended maternal contact, elicits heightened distress in both human and rodent infants (Shair et al., 2015). One explanation for this effect is that insufficient time with the mother leaves a hunger like state in the offspring which is blunted if the contact is of sufficient duration to satiate a social need. Likewise, compensatory increases in play behavior have been observed in

juvenile rats following periods of social separation, and the longer the separation the more play behavior is expressed. This suggests that rats are motivated to obtain a certain amount of play in this specific developmental phase (Panksepp et al., 1984).

The role of motivation in guiding phase-specific social behavior is also suggested by several studies indicating that when new targets of social behavior emerge, the motivational response to previous social categories diminish. For instance, the duration and intensity of distress during maternal separation declines across infancy for a number of species at the same time that play behavior increases (Hinde and Spencer-Booth, 1967; Barr, 1990; Brunelli and Hofer, 1996; Zhang et al., 2012). Likewise, a recent study in humans demonstrated that maternal presence can blunt the cortisol stress response in young pre-adolescent children, but has no effect on adolescents, who have shifted their motivated behavior toward peer integration (Hostinar et al., 2015). Finally, peer group directed behavior becomes less important for adolescents and young adults after romantic engagements have become established (Collins et al., 2009). Taken together, these data provide evidence that suggests the focus of social goal undergoes systematic shifts across development, and is accompanied by changes in motivation to obtain and maintain specific types of social experience.

Another feature of social behavior within each developmental phase is that the behaviors themselves are malleable and become adapted to the local social environment. This is perhaps most clearly demonstrated in the emergence of face processing biases. A classic example of this phenomenon was demonstrated in cross-species comparisons of face recognition capabilities during the first year of life. While motivation to attend to face-like stimuli is present at birth, experiences during the early infancy phase sculpt subsequent face-processing capabilities. For example, at six months of age, humans and monkeys demonstrate equivalent capacity to recognize differences between individuals of both species. However, over the course of the following six months, recognition capabilities for individuals of one's own species increases while similar capabilities for other species diminishes (Pascalis et al., 2002). Hence, a same-species bias emerges in perceptual processing as a consequence of social experience. Similar tuning of social perception has also been characterized for specific facial features associated with race, gender, and age (Scherf and Scott, 2012). Each processing bias appears to be sculpted by specific contextual experiences during unique developmental windows.

A similar perceptual-tuning process may also occur in the auditory domain. Despite being pre-linguistic, infants are able to respond selectively to emotional content in voices from an early age (Grossmann et al., 2010), and recognize identity based on vocal characteristics. However, these biases are only observed when the speaker uses the infant's native language (Johnson et al., 2011). This suggests that, like experience-tuned biases in face processing, maturation-related biases in voice processing are molded by the contexts a child experiences (Perrachione et al., 2011).

Another example of this context-matching aspect of social behaviors in development can be found in juvenile play. While anthropological studies have revealed that both physical and imaginary play in virtually all human cultures peaks during middle childhood (Konner, 2010), the form that the play takes can vary markedly across cultures. In some cultures, play involves ritualistic dance, in others it has more elements of hunting and chasing, and in still others it involves pretending to take on different adult roles (Whiting and Edwards, 1992; Rogoff, 2003; Konner, 2010). Similarly, during adolescence, adaptation to the peer group often involves adoption of specific cultural norms expressed by specific local groups into which they are attempting to integrate (e.g., “goths” vs “jocks”) (O'Brien and Bierman, 1988). These findings suggest that while there is a developmentally specific aspect in the timing of learned social behaviors, the specific form of that

expression is strongly molded by the particulars of environmental conditions.

Although specific motivated behaviors and adaptive responses are unique to each social phase, it is clear that experiences in each phase are interdependent insofar as their effects cascade into successive periods. The experiences that occur in each phase may impact the expression of social behaviors and motivations in subsequent phases. For instance, experiences with a caretaker in infancy can moderate social behavior with peers in adolescence, and parenting style with offspring in adulthood (Fleming et al., 1999; Kumsta et al., 2012; Olsavsky et al., 2013). Studies on play behavior have indicated that play experience in the juvenile period may promote flexibility and enhanced cortical function in adult social contexts (Fagen, 1981; Himmler et al., 2014). Additionally, competence with peers in adolescence is predictive of romantic competence in adulthood (Roisman et al., 2004). Thus, while each new social phase in development generates a shift in motivational direction, behavioral re-organization, and adaptation to localized experiences, these experiences can have both short and long-term consequences on subsequent behavior which is likely mediated by sustained changes to underlying neural circuits.

3. Sensitive periods and the role of the environment in canalizing maturation

Conceptualizing maturation in terms of distinct phases, each with specific socially motivated goals, is not a novel concept. In fact this has been the foundation for various theories of human development for generations (Havighurst, 1972; Erikson, 1993; Masten et al., 1995; Roisman et al., 2004). Stage based approaches also appear in “dynamic systems approaches” to maturation, in which development is construed in terms of system-wide integrated adaptation to emerging and shifting environmental contexts or niches (Gubernick and Alberts, 1984; Thelen and Smith, 1994; Barr et al., 2009; Johnson, 2010; Scherf and Scott, 2012). Such approaches tend to run counter to reductionism of neuroscience, where mechanisms are often stripped of contextual function. More recently, however, integrative models that incorporate dynamic change across maturation have begun to emerge in developmental cognitive neuroscience as well (Crone and Dahl, 2012; Scherf and Scott, 2012; Scherf et al., 2013; Nelson et al., 2014).

One concept in developmental neuroscience that resonates with stage approaches common in developmental psychology is that of sensitive or critical maturational periods. In this approach, brain and behavioral organization are considered particularly amenable to specific types of information during specific developmental windows (Nelson and Panksepp, 1998; Bell et al., 2010; Meaney, 2010; Nelson and Guyer, 2011; Crone and Dahl, 2012; Takesian and Hensch, 2013; Nelson et al., 2014). Sensitive period models of brain development generally regard neuronal circuit maturation as a confluence of endogenous maturation and experiential sculpting. When neural systems begin to mature, they are weakly responsive to a wide scope of stimuli, and generate diffuse patterns of activation within and between other circuits. However, this pattern changes as experience with categorical exemplars accumulates. Brain responses become stronger, more efficient, and automatic as the boundaries of relevant stimuli become narrower, while responses to non-experienced stimuli are dampened (Greenough et al., 1987; Knudsen, 2004; Stiles, 2008; Leppanen and Nelson, 2009; Werker and Hensch, 2015).

Interestingly, while the timing of the opening and closing of sensitive windows has generally been considered an internally mediated phenomenon with pre-determined timing parameters, under some conditions, environmental experiences can also affect the timing and pace of the period of heightened sensitivity. For

example, in animal models, complete light restriction prolongs the closing of the window for organization of the visual cortex (Johnson, 2005), while restricted physical exposure to conspecifics can delay the closing of sexual imprinting (Bischof et al., 2002; Bischof, 2007) and delay the narrowing of face perception capabilities (Sugita, 2008). In humans, several factors, including body weight and life stress, influence the timing of puberty onset (Ellis et al., 2011; Lee and Styne, 2013). Moreover, recent findings suggest that the timing of neural circuit organization during human development may also be susceptible to extreme differences in environmental conditions, whereby brain maturation may be accelerated in order to facilitate social goals in the face of adversity (Gee et al., 2013). Although the extent to which environmental influences affect timing parameters of brain development has not been extensively investigated, particularly in humans, the existing data are suggestive of this being an important factor to consider in future studies.

Advances in research on molecular contributions to developmental plasticity may inform our understanding of factors that contribute to the onset and offset of sensitive periods during both early life and later phases, as cortical organization continues to occur (Blakemore, 2014). For instance, recent studies indicate that changes in the plasticity of local circuits are dependent on the maturation of local inhibitory connections, which may regulate sensitive periods at a molecular level by shifting the local excitatory–inhibitory balance within local circuits (Takesian and Hensch, 2013; Werker and Hensch, 2015). Isolating regionally specific markers for heightened plasticity across sensitive periods in development may help us understand how neural organizational sculpting influences specific social functions during different phases of development. In addition it may be possible to re-open a closed critical period with targeted pharmacological approaches (Gervain et al., 2013). The difference between these mechanistic approaches to developmental periods and more traditional holistic stage-based approaches in developmental psychology may be simply a matter of semantics or scale. An important point of emphasis in both approaches, however, is that experiences are not uniformly effective in inducing change across maturation. Rather the degree to which different experiences can affect developmental trajectory depends to a large extent on when in the trajectory the experiences occur.

4. Developmental changes in perceptual regions

One approach to better understanding how social behavior emerges across development is to characterize the neural circuitry that mediate cognitions, emotions, and behavior as they mature. Although some of the basic neural systems engaged by social processing are functional in infancy, others come online only later in development. Developmental changes in the neurobiological substrates engaged by social stimuli have been the focus of many neuroscience studies in recent years. We will provide an overview of this work and suggest some generalizations that can be made from this literature to date.

As described above, one of the three key features of social cognition is perceptual. The ability to categorize, recognize, and appraise a social stimulus is critical for generating social behavior. Within the perceptual stream, developmental studies have generally found support for several patterns. First, social stimuli are highly salient for infants and a remarkable ability to perceptually process social stimuli is evident from early in life. Second, there is good evidence for experience expectant tuning of brain responses to some social stimuli which also occurs early in life. Third, in spite of the fact that social perception capabilities are grossly competent in infancy, a protracted period of refinement in these capabilities lasts through at least late adolescence and likely into middle adulthood.

Face processing, or the ability to extract information such as emotional expression, group membership, and identity from a face, is a prototypical perceptual function. Soon after birth, infants demonstrate attentional orienting toward faces, facial features like eyes, and displays of biologically based movement (Simion et al., 2008; Leppanen and Nelson, 2009; McKone et al., 2012; Senju et al., 2013; Bidet-Ildei et al., 2014). Directing attention to the eyes may be a congenital feature as even infants of blind parents, for whom eyes contain no inherent social information, tend to focus on the eyes (Senju et al., 2013). Infants also orient toward voices – especially of their caretakers (DeCasper and Fifer, 1980; Grossmann et al., 2010), and are able to discern some emotional content contained in voices.

In recent years, a growing body of research on face processing in both humans and nonhuman primates has demonstrated that perceptual processing occurs in several distinct areas of occipital and temporal lobes. This includes the occipital face area (OFA), fusiform face area (FFA), and several other regions across the superior temporal sulcus (STS) and inferior temporal lobe (IT) (Freiwald and Tsao, 2010; Goesaert and Op de Beeck, 2013; Morin et al., 2014; Pitcher et al., 2014; Hung et al., 2015; Weiner and Grill-Spector, 2015).

In general, neural processing of social percepts advance along the temporal lobe in a step-like fashion, with each step adding an increasing degree of integration of the various salient aspects of the stimulus such as identity, gaze direction, and emotional expression (Morin et al., 2014). Increased integration is the result of brain regions directly related to face processing, but also other regions that are engaged by affective and goal-related processes, such as amygdala and prefrontal cortex (Fusar-Poli et al., 2009; Cohen Kadosh et al., 2010; Freiwald and Tsao, 2010; Hadj-Bouziane et al., 2012; Morin et al., 2014). As the neural percept advances along the rostral axis of the temporal lobe, integration results in a neural signal that is increasingly invariant, combinatorial, and holistically representative of the stimulus.

Similar regions in the temporal lobe have also been implicated in the perceptual processing of other key features of social stimuli including specific body parts, speech, and biological motion (Schwarzlose et al., 2005; Galvan et al., 2007; Peelen et al., 2009; Belin and Grosbras, 2010; Grossmann et al., 2010; Perrachione et al., 2011). Although much less work has been devoted to the neural systems engaged during processing of social stimuli from these domains, similar stepwise hierarchical processes may also occur with these functions as well. However, faces are particularly powerful for human social interaction. Thus, it is worth noting that differences have been found in the developmental trajectory between face and body processing across maturation (Peelen et al., 2009).

While many studies have demonstrated that gross levels of competence in social perception are evident very early in life, other findings have shown that maturational changes continue for a substantial period of time. Indeed, in a study that included 60,000 participants from a wide age range, Germine et al. demonstrated that facial recognition capabilities continue to improve through age 30 (Germine et al., 2011). Other capabilities such as the ability to use configural relations among facial features and to flexibly attend to different aspects of the face stimulus also continue to improve through the adolescent period (Mondloch et al., 2006; Cohen Kadosh et al., 2013a).

Structural imaging studies have indicated that developmental modifications continue to occur in occipital and temporal lobes including FFA, STS, and TPJ through at least the late adolescent period (Blakemore and Mills, 2014). Indeed, the temporal lobe is one of the latest to reach maturity (Gogtay et al., 2004). These structural changes generally reflect relatively large scale increases in brain volume and gray matter intensity during the first several years of life, followed by a more gradual reduction in gray matter,

and a subsequent increase in white matter in late juvenile and early adolescent phases (Mills et al., 2014). Developmental differences in behavioral sensitivity and functional activity within social perception regions likewise suggest a developmental profile of large scale changes during early life followed by more subtle refinements that continue into adulthood.

Neuroimaging studies have shown that regions such as the FFA, STS and TPJ show selectivity for social stimuli by early childhood if not sooner. However, changes in the patterns of activation, and in the networks associated with activation of these perceptual regions, continue to occur through at least late adolescence (Carter and Pelphrey, 2008; Guroglu et al., 2011; Johnson, 2011; Pfeifer and Blakemore, 2012; Pfeifer and Peake, 2012; Cohen Kadosh et al., 2013b; Blakemore and Mills, 2014). For example, face sensitive regions have been shown to increase in both spatial extent and response magnitude through adolescence (Aylward et al., 2005; Golarai et al., 2007; Scherf et al., 2007). These changes have been attributed to both age and pubertal status (Moore et al., 2012).

As the face response network extends to other regions of the brain, it also becomes more flexibly engaged during different goal states. For example, task demands elicit developmental differences in brain function during face processing through early adulthood (Cohen Kadosh et al., 2010, 2013c). Whether a face is being scanned for purposes of identity, emotional content, or feature detection influences the extent to which perceptual regions co-activated with other networks (Cohen Kadosh et al., 2010; Johnson, 2011; Cohen Kadosh et al., 2013a). During social perception tasks, increased functional connectivity has been observed with non-perceptual regions with increased age (van den Bos et al., 2011; Pfeifer and Blakemore, 2012; Cohen Kadosh et al., 2013b). However, this may depend in part on demands of the task and strategy adopted by the subjects (Cohen Kadosh et al., 2010; Moor et al., 2012; Cohen Kadosh et al., 2013c). Scherf and Scott have suggested that developmental differences in engagement patterns may reflect differences in social demand. For instance, the most important social signals during the juvenile phase may relate to valence, but during the peer integration phase of adolescence social features that tap social cognition processes like dominance and trustworthiness may become more important (Scherf and Scott, 2012).

In summary, the regions involved in social perceptual processing such as the FFA, STS and TPJ undergo developmental changes that reflect an innate sensitivity to inherently salient social stimuli. During infancy and early childhood these regions are fine-tuned to respond to specific features in the social world. Then, over the course of a decades long protracted developmental process, functional responses in these brain regions become increasingly networked and integrated with other maturing neuronal components, culminating in a highly refined, adaptive, and flexible system.

5. Developmental changes in affective/motivational regions

In human neuroimaging studies, the most prominent structures implicated in social affect and motivation are the amygdala and striatum, ventral prefrontal cortex, and anterior insula. The animal literature has identified a much more extensive network of regions involved in the expression of emotional or motivational behavior within social environments including the hypothalamus, bed nucleus of the stria terminalis, and brain stem regions (Panksepp, 1998). This discrepancy is most likely due to limitations of neuroimaging techniques, rather than a fundamental difference in brain structures mediating social emotions between animals and humans. It is clear that the amygdala and striatum, in particular, interface with both perceptual regions in temporal lobe (Hadj-Bouziane et al., 2008; Cassia et al., 2009; Hadj-Bouziane et al., 2012; Miyahara et al., 2013; Haeger et al., 2015) and executive systems in

prefrontal cortex (Guyer et al., 2008a; Crone and Dahl, 2012; Guyer et al., 2012; Jarcho et al., 2015a; Smith et al., 2015) to guide social behavior under varying conditions. In contrast to the developmental changes in the perceptual regions, which can be characterized as early large scale organization followed by protracted refinement, the most consistently reported developmental profile of both the amygdala and striatum is an inverted U-shaped pattern in which responsiveness to social stimuli increases from the late juvenile phase into adolescence, and then diminishes again from adolescence into adulthood (Guyer et al., 2008b; Hare et al., 2008; Galvan, 2010; Somerville and Casey, 2010; Chein et al., 2011; Spear, 2011; Scherf et al., 2013; Somerville et al., 2013). However, this pattern is not always observed (Spear, 2011; Crone and Dahl, 2012; Pfeifer and Allen, 2012). For example, a linear decrease has been reported in amygdala response to unfamiliar adult faces between early childhood and mid adolescence (Tottenham et al., 2012), and several studies have found relative increases between adolescents and adults in activity of both striatum and amygdala in response to various social stimuli (Ernst et al., 2006; Carter and Pelphrey, 2008; Guyer et al., 2009; Bjork et al., 2010; Galvan, 2010; Gunther Moor et al., 2010; Scherf et al., 2013; Casey et al., 2014).

Indeed a key feature of our revised framework is that, in regards to social processes, the activity of both amygdala and striatum vary as a function of stimuli, context, and task demands. Activity from the subcortical, affective, and motivation-related regions generate intrinsic salience signals, which highlight distinct experiences or stimuli that are *developmentally relevant* in the social environment (Leppanen and Nelson, 2009; Scherf et al., 2013; Nelson et al., 2014). Similar models have been suggested by Scherf in relation to developmental changes in face processing (Scherf and Scott, 2012; Scherf et al., 2013). Salience signals from subcortical limbic structures may guide approach and engagement or withdrawal and avoidance behaviors, or may simply direct cognitive systems such as attention and memory toward developmentally appropriate social cues without inducing affective change (Leppanen and Nelson, 2009). These salience signals also promote networking between perceptual systems and other brain regions related to motivation and behavioral execution. We suggest the primary function of affective engagement in development is to influence neural circuit formation during sensitive organizational periods (Cohen Kadosh and Johnson, 2007; Cohen Kadosh et al., 2013a, 2014; Scherf et al., 2013; Jarcho et al., 2014). From a more general perspective, rodent studies have found a developmental trend in both brain activation and behavioral responses that are elicited from widespread and nonspecific activation to more refined and selective responses (Wiedemayer, 2009; Simon and Moghaddam, 2015). This change is probably a reflection of both maturation and experience (Wiedemayer, 2009).

In the context of the five social phases, this pattern should be reflected in amplified (and more extensive) signals to the mother in infancy, to peer play in juvenile development, to peer acceptance and integration in adolescence, and to romantic or close intimacy signals in late adolescence. Some support has been found for these predictions in animal studies, although this hypothesis has not been extensively tested in neuroimaging paradigms. For example, differential patterns of amygdala activity were evident when monkeys were separated from their mother at 1 week vs one month of postnatal life (Sabatini et al., 2007). This differential amygdala response correlated with a distinct social behavioral profile later in development (Sabatini et al., 2007), suggesting age specific tuning of behavioral profiles mediated by specific amygdala response patterns. Another example of this phenomenon can be found in the rodent literature. In rats, social play is a highly motivated experience that engages many regions of the brain including the striatum, amygdala, and thalamus (Trezza et al., 2010; Siviý and Panksepp, 2011). The experience of social play during the juvenile phase appears to affect the maturation of the medial prefrontal

cortex, and the flexible engagement of this region in social encounters later in development (Bell et al., 2010; Himmler et al., 2013, 2014). Different types of play experience at distinct developmental periods may therefore differentially shape both brain and behavior in adulthood.

While the proposed role of subcortical signals in sculpting cortical patterns in development is admittedly speculative, there is some support for a similar process in the animal learning literature. In a motivated learning context, responses in ventral striatum, amygdala, and hippocampus have been shown to subside as habitual responses and memory consolidation emerge. Control of behavior and orchestration of distributed memory networks is thought to shift from ventral to dorsal striatum or from hippocampus to dorsal prefrontal cortex for example (Vanderschuren et al., 2005; Euston et al., 2012; Clark et al., 2013). If subcortical emotion related structures serve as a signal to guide formation of interconnected circuits, one might expect to see not only differences in sensitivity, but also patterns of structural and functional connectivity with other regions. While the systematic investigation of developmental changes in functional connectivity has only just begun, several findings provide support for the presence of age-related changes in connectivity. Age-related increase in PFC coupling occurs for both the amygdala and ventral striatum, in both a threat assessment and a social evaluation context during adolescence (Guyer et al., 2008a; Pfeifer et al., 2011; van den Bos et al., 2012; Somerville et al., 2013; Spielberg et al., 2014a, 2015). This suggests an important anatomical mechanism for integrating salient signals across development.

While there are a number of reports of *enhanced* coupling between subcortical and cortical structures in adolescence, there have also been some reports of a *decrease* in functional coupling between amygdala and orbitofrontal activity in adolescence (Spielberg et al., 2014b). Our framework suggests that stimulus or task demands are another critical feature impacting differences in connectivity observed across maturation. Tasks that are developmentally relevant (e.g., play for juveniles, peer acceptance for adolescents) would likely result in transient increases in coupling, while those that are not developmentally relevant may result in transient decreases; both would impact the way in which environmental stimuli are processed across development.

One important task for future developmental studies is to identify the mechanisms that mediate developmental shifts in affective responding. Some of changes in affect/motivation-related brain responses appear to be linked to physiological events (e.g., the effect of sex steroids on brain function) (Forbes and Dahl, 2010; Op de Macks et al., 2011; Crone and Dahl, 2012; Scherf et al., 2013; Spielberg et al., 2014a, 2015), whereas others may relate to different salient developmental events like weaning or transition into novel social contexts (Sullivan and Holman, 2010). An interesting corollary to the effects of sex steroids on limbic system responses in puberty is in rat pups, maternal presence, and suckling in particular, has an inhibitory effect on cortisol secretions and the HPA axis. As the relationship with the mother changes, infant rats move out of the stress hypo-responsive period, begin secreting cortisol in response to stressors and gain the capability of forming aversive associations with odors (Sullivan and Holman, 2010). This relationship is thought to be mediated by the effects of cortisol on amygdala function (Sullivan and Holman, 2010).

In an influential model, which differs to some extent in the details of our own model, but results in similar proposed modifications of developmental learning, Crone and Dahl have argued that in adolescents, pubertal steroids temporarily disrupt some of the top-down inhibitory controls on subcortical activity, which results in both greater emotionality and reduced automaticity in task completion. This, in turn, may promote more flexible and adaptive problem solving in adolescence (Crone and Dahl, 2012;

Spielberg et al., 2014b), and facilitate individually tailored long term behavioral solutions. Regardless of the specific model, there is a growing consensus that changes in subcortical responding to social stimuli take place across development, and these changes impact and guide adaptive circuit formation in social development in important ways.

Several recent studies have also found evidence for “lingering” effects of differential experiences in previous developmental periods on concurrent responses to social stimuli. Positive emotional parenting in childhood has been associated with attenuated growth of amygdala and accelerated cortical thinning in ventral prefrontal regions in adolescents (Whittle et al., 2014). Functional studies have found that negative parenting blunts responses to peer acceptance in several regions including amygdala, striatum, and anterior insula, whereas constructive authoritative parenting is associated with a blunted caudate response to peer rejection (Tan et al., 2014; Guyer et al., 2015). Finally, Gee et al. have shown that rearing under conditions of extreme deprivation can fundamentally alter the relationship between the amygdala and the prefrontal cortex much later in development (Gee et al., 2013). Taken together, while interactions between emotional systems and both executive and perceptual systems play an active role in guiding development within each maturational phase (Field et al., 2009), the responsivity of these regions themselves is sensitive to social experiences that occurred in previous phases of development as well.

6. Developmental changes in executive systems

Executive functions (EFs), such as voluntary attention control, intentional response selection, or contextual framing of stimuli, serve to guide behavior, attention, and memory toward or away from predetermined goals. EFs interface with perceptual systems to enhance or blunt sensory processing of stimuli (Shi et al., 2014). EFs can also augment or diminish emotional experience and associated subcortical signals (Ochsner et al., 2004; Giuliani et al., 2008). Conversely, emotional activity can diminish efficacy of executive functions when they are irrelevant to task demands, or enhance functioning when they are congruent with them (Blair et al., 2007; Robinson et al., 2013). EFs have a protracted developmental trajectory. For example, improvements in working memory, selective attention, response inhibition, and flexible engagement of behavior occur from birth through the mid to late adolescent years (Luna et al., 2004; Crone, 2009; Luna, 2009; Diamond, 2013). This improvement is particularly marked in the social domain (Germiné et al., 2011; Gur et al., 2012). A similar protracted and largely linear developmental pattern has been observed specifically in the ability to use EF to modulate emotional responses (McRae et al., 2012).

EFs are instantiated in dorsal, medial, and ventrolateral regions of prefrontal cortex (Miller and Cohen, 2001). However, the ventral region of PFC, which includes the orbitofrontal cortex, plays more of an intermediary role between “hot” functions, like subjective valuation, and “cold” executive functions like response selection (Rudebeck et al., 2013). Similarly the anterior cingulate cortex (ACC), while not traditionally viewed as a region directly involved in cold executive functions, plays an important role in cognitive control, particularly in the context of affective experiences, learning, and error monitoring (Totah et al., 2009; Medalla and Barbas, 2010; Shackman et al., 2011; Tamnes et al., 2013). A number of studies have indicated that the ACC and vPFC play an important role in various aspects of social interaction (Somerville et al., 2006; Guyer et al., 2008b; Masten et al., 2009, 2011; Somerville et al., 2013; Blakemore, 2014; Guyer et al., 2015; Jarcho et al., 2015a,b). These regions might play a particularly important role in integrating social behavior with more traditional (cold) EFs.

Both structural and functional maturational changes in the PFC occur into late adolescence in humans (Gogtay et al., 2004; Crone, 2009; Luna et al., 2010; Mills et al., 2014). From a structural standpoint, the PFC matures in a manner similar to the social perception regions in the occipital and temporal lobe. In early life there is an increase in volume and gray matter, followed by a more protracted reduction in gray matter, and a linear increase in white matter. Functionally, however, there may be important differences in development between perceptual and executive mechanisms. As indicated above, while several “sensitive periods” have been identified for social perceptual processes, like face processing and language acquisition, no such windows have been identified for EFs in the social domain (but see Nelson et al. (2007) for a possible exception).

Rather than develop in a pattern of rapid orienting and protracted narrowing and refining, EFs tend to develop in a manner suggesting slow linear improvement of function as the brain matures with age (Gur et al., 2012; Tamnes et al., 2013). This relatively slow improvement in EFs may help explain the protracted and gradual ability to match social behavior to specific goals and task demands (Cohen Kadosh et al., 2013b). It may also reflect the gradual transition of motivated behavior across different phases of development into individualized patterned circuits (Euston et al., 2012). Several models contrast the slow linear maturation of brain regions implicated in EF with the inverted-U shaped maturational pattern of brain regions implicated in affective processing in general (Ernst et al., 2006; Somerville et al., 2010), and affective processing in the social domain in particular (Steinberg, 2008; Smith et al., 2013). These models have generally highlighted the transition from adolescence to adulthood as a risky period when behavioral responses are strongly impacted by affective responses since EF systems reach full functional maturation in adulthood.

While there is much evidence for a protracted functional maturation of EFs and a mismatch in maturation of brain regions supporting affective and cognitive control processes, a strict linear transition from hot affective to cold executive control of social behavior seems unlikely in the face of changing affective response profiles highlighted above. The fact that EFs interact with affective response systems rather than simply controlling them, and the complex maturational profile of social affect across development, we suggest a more nuanced developmental profile of EFs in the context of social behavior. While “cold” EFs are likely to guide social behavior to a greater extent across development, factors such as the specific emotional context (playmates vs peers integration vs romantic partner), and whether EFs are congruent or incongruent with this context, are likely to be important factors as well.

Finally, within the context of social development, one of the more consistent findings is a decrease in medial and dorsal PFC activity during the transition from adolescence to adulthood. These differences have been observed in response to tasks that involve face processing, mentalizing, accessing social knowledge about self and others, and socially interactive decision making (Blakemore, 2008; Burnett et al., 2011; van den Bos et al., 2011; Blakemore, 2012; Pfeifer and Blakemore, 2012). There is also some evidence for an increase in mPFC and dPFC activation between childhood and adolescence, which precedes this decline (Pfeifer et al., 2011). Thus, under many conditions, the PFC and subcortical structures may have a similar inverted U-shaped developmental profile. However, the developmental changes across these two domains are not a unitary process. In fact, discontinuity or segregation between prefrontal and subcortical activity may underlie some aspects of aberrant adolescent behavior (Ernst et al., 2006). As with both the perceptual and affective regions discussed above, the specific dynamics of EF development, as well as the interaction between PFC, affective, and perceptual regions, are highly dependent upon stimulus, context, and task demands (Pfeifer and Allen, 2012).

Given the dynamic nature of these systems, one should be careful not to overgeneralize or oversimplify this process.

From a functional development perspective, the decline in PFC activity during the transition from adolescence to adulthood tends to coincide with a relative increase in functional activity in posterior regions of the brain, such as TPJ and pSTS (Pfeifer and Blakemore, 2012). This may reflect a general principle of rostral–caudal maturation, or the emergence of more automaticity in the execution of socially oriented behaviors like mentalizing or face processing functions. Both enhanced skill proficiency and experience with diverse functional networks may result in less need for effortful EF engagement across development (Johnson, 2001; Pfeifer and Blakemore, 2012). Learning and the establishment of habitual patterns of social behavior are likely to be an important feature of development (Jarcho et al., 2015b), and this transition may be a reflection of this process. However, this may also result in less flexibility and compromised ability to adapt to changing social conditions (Crone and Dahl, 2012).

7. Summary and conclusions

Although social behavior is embedded in many diverse contexts, there are some generalizations about development that can be made. First, although social engagement is highly motivated across the lifespan, the object of social motivation and the structure of social behavior change markedly across development. In the early years, the primary focus of social motivation is contact with the caretaker. Social behaviors then transition to peer play in the early juvenile period, to peer acceptance and integration in early adolescence, and to romantic intimacy in later adolescence. From the neural standpoint, most social behavior involves activation of complex networks. We have construed these networks as belonging to three functional areas – those involved in perceptual and sensory processing of the stimulus; those involved in coding the value or affective significance of the stimulus to the individual; and those involved in executive functions related to the effortful manipulation of the stimulus and integration with other cognitive and behavioral functions.

In the framework outlined in the present paper, we have argued that changes occur in all three of these regions throughout development as nested within age-dependent social demands. Perceptual systems are inherently responsive to social stimuli, and postnatal brain development proceeds in two steps. Rapid, large scale tuning occurs in early postnatal life upon exposure to species specific exemplars; more refinements and integration then continues through early adulthood (Leppanen and Nelson, 2009). In contrast, maturation of brain activation within the affective domain corresponds with shifting patterns of social salience and behavioral engagement. Thus, subcortical structures may be most sensitive to cues related to the mother in infancy and toddlerhood, to peer play in the juvenile period to peer acceptance in early adolescence and to intimacy in late adolescence, and ultimately to care of offspring in adulthood. These “bottom up” signals may engage both EFs in prefrontal cortex and sensory/perceptual systems in the occipital and temporal lobes (though connectivity is likely bidirectional). What factors contribute to the transfer of salience attribution associated with the phase shifts are largely unknown, although steroids and learning may contribute. Characterizing the factors that contribute to phase shifts is an important task for future developmental studies. Finally, the executive systems, which display a particularly protracted pattern of maturation, exhibit a decrease in functional activity during social tasks, particularly across the transition from adolescence to adulthood. This decrease may correspond with the emergence of habitual and/or flexible patterns of social behavior or less effortful activation of social/perceptual systems for the

completion of social tasks. Thus, these three functional processes act in concert to tune different social behaviors at different points in development contingent on the demands of that phase.

The sensitive period model of social development may have important implications for understanding and treating psychopathology. Most chronic mood and anxiety disorders first appear during juvenile or adolescent development, and often have a strong social component (Pine et al., 1998; Kessler et al., 2005; Paus et al., 2008). Although the sensitive period framework emphasizes the importance of affective experiences in shaping brain networks, this shaping can be either adaptive or maladaptive for adult functioning. Considerations of how affective reactivity changes across development and is integrated with changes in executive and perceptual systems across development are likely to have important treatment implications (Monk, 2008). Thus the phase of social development and the timing of social experiences will likely play an important role in the efficacy of different types of intervention.

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